

Effects of Insect-Vector Preference for Healthy or Infected Plants on Pathogen Spread: Insights from a Model

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J. Econ. Entomol. 101(1): 1–8 (2008)

ABSTRACT Insects vector many plant pathogens and often have higher or lower densities on infected plants than on healthy plants. Two hypotheses may explain this observation: insects may preferentially orient toward and select one plant type (referred to as orientation preference) or insects may reside on infected plants for longer or shorter periods than on healthy plants (referred to as feeding preference). The effects of feeding preference and orientation preference were compared alone and in combination using a spatially explicit model. With feeding preference for healthy or infected plants, the qualitative relationship between the percentage of plants infected and the rate of pathogen spread was not affected. However, feeding preference for healthy plants increased rates of pathogen spread, whereas feeding preference for infected plants decreased rates of pathogen spread. Unlike feeding preference, orientation preference for healthy and infected plants produced qualitatively different relationships between the percentage of plants infected and the rate of pathogen spread. With orientation preference for healthy plants, the pathogen spread slowly when few plants were infected, but quickly once most plants were infected. In contrast, with orientation preference for infected plants, the pathogen spread quickly when few plants were infected, but slowly once most plants were infected. In sensitivity analyses, we found that assumptions about the latent period (time between infection and when insects can recognize a plant as being infected) and persistence (length of time an insect remains inoculative) altered the aforementioned effects in some cases. The results illustrate that feeding and orientation preference affect pathogen spread differently, highlighting the importance of elucidating the mechanisms that control vector preference for healthy versus infected plants.

KEY WORDS disease management, epidemiology, insect vector, modeling

Insects vector many plant pathogens. Such insects locate and accept plants based on a range of cues produced by the plant. Infection of a plant by a pathogen may alter these cues making the plant more or less attractive to the vector. Indeed, insects have been found to prefer infected plants (Baker 1960, Macias and Mink 1969, Eckel and Lampert 1996, Castle et al. 1998, Eigenbrode et al. 2002, Musser et al. 2003, Jiménez-Martínez et al. 2004, Maris et al. 2004, Srinivasan et al. 2006), healthy plants (Blua and Perring 1992, Shykoff and Bucheli 1995, Altizer et al. 1998, Fereres et al. 1999, Marucci et al. 2005), to have no preference (Castle et al. 1998, Fereres et al. 1999), or to initially prefer one type and then switch to another (Khan and Saxena 1985). Such interactions are not unique to insect-vector plant-pathogen systems. Insect vectors of animal pathogens also have been shown to prefer hosts based on their infection status (Lacroix et al. 2005, Nacher 2005).

Typically, preference for or aversion to infected plants is established by releasing insects in cages with

healthy and infected plants and counting the number of insects on each plant type. Although such a design can establish the relative preference of an insect for infected or healthy plants, it indicates little about the mechanisms controlling this choice. Two hypotheses could account for differences in insect density on healthy and infected plants. First, insects may preferentially select infected or healthy plants based on visual or olfactory cues (referred to as orientation preference). For example, preference for infected plants is often hypothesized to be due to the yellowing of leaves caused by infection (Ajayi and Dewar 1983, Eckel and Lampert 1996, Fereres et al. 1999, Marucci et al. 2005). An alternative hypothesis is that insects reside on healthy or infected plants for longer or shorter periods of time in response to gustatory cues (referred to as feeding preference). Indeed, some studies have inferred that feeding is required for insects to differentiate between healthy and infected plants (Macias and Mink 1969, Blua and Perring 1992). Importantly, acquisition and transmission of the pathogen is not possible during the discrimination phase if orientation cues (i.e., visual or olfactory) are

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solely used to differentiate between healthy and infected plants. However, acquisition and transmission of the pathogen is possible during the discrimination phase if gustatory cues are used to differentiate between healthy and infected plants. Consequently, it is likely that these two types of preference affect pathogen spread differently.

The effects of insect preference for healthy or infected plants on pathogen spread have received limited theoretical attention. Most notably, McElhany et al. (1995) examined the effects of preference for infected or healthy plants on pathogen spread using a variety of models and demonstrated that insect preference can have important effects on pathogen spread. However, McElhany et al. (1995) did not consider the effects of “feeding preference” and “orientation preference” separately. Nor did they consider interactions with other parameters. Here, a simple spatially explicit model based on that of McElhany et al. (1995) is used to illustrate that “feeding preference” and “orientation preference” affect pathogen spread differently. The results emphasize the need for empirical studies to elucidate the mechanisms responsible for insect preference. A sensitivity analysis also was completed to determine which parameters alter the effects of preference on pathogen spread.

Methods

Model Structure. The model was written in C++ (Microsoft Visual C++ 2005), and it is similar to the stochastic, spatially explicit model of McElhany et al. (1995) (code available on request). The model is simple and the assumptions general. Thus, the results are discussed in a broad context. Table 1 summarizes key assumptions. A single field with 60 rows and 60 plants per row (60 by 60 = 3,600 plants) was modeled. As in McElhany et al. (1995), insect population dynamics was ignored, and a fixed number of insects, which neither died nor produced offspring, was introduced to the field at the start of each simulation. During each time step, each insect could move to a new plant, acquire the pathogen from an infected plant, and, if the insect was inoculative, transmit the pathogen to a healthy plant. The length of a time step represented the average time over which a movement decision was made.

Default Movement. Without either type of preference, the probability that an insect moved to a new plant was the same for healthy and infected plants, and the default value was 0.10 (Fig. 1A, no preference). To determine whether an insect moved, a random number between 0 and 1 was obtained for each insect. The insect moved to a new plant if the random value was less than the probability that the insect moved, otherwise, the insect remained on that plant until the next time step. If an insect moved, a new plant was selected within the insect’s local search area. The local search area was defined as all plants within a distance of six plants in any direction from the insect’s current location. Insects were equally likely to move within or between rows. Without orientation preference for

Table 1. Parameter values used for default simulations and sensitivity analysis

Parameter	Value ^a
Plants per field	3,600 (60 rows × 60 plants per row)
Initial percentage of plants infected	0
Persistence ^b (times steps)	2, indefinitely*
Latent period ^c (time steps)	1*, 30, 60
Probability of acquisition (per time step)	0.05, 0.50*, 0.95
Probability of inoculation (per time step)	0.05, 0.50*, 0.95
Probability an insect moves to a new plant	0.01, 0.10*, 0.25
Size of local search area	6 plants in all directions
Insect density (per plant)	0.1, 1*, 10
Initial percentage of inoculative insects	0.027*, 2.77

^a Default values are indicated by an asterisk.
^b Persistence is the length of time an insect remains inoculative.
^c The latent period is the time between inoculation and the onset of symptoms. Insects can only acquire the pathogen from symptomatic plants and cannot discriminate between asymptomatic infected plants and healthy plants.

healthy or infected plants, the probability that an infected plant was chosen in the local search area was equal to the frequency of infected plants in the local search area (Fig. 1B, no preference). Insects were not allowed to move out of the field.

Feeding Preference. To simulate feeding preference, insects were assumed to evaluate the plant during feeding and the probability they remained on that

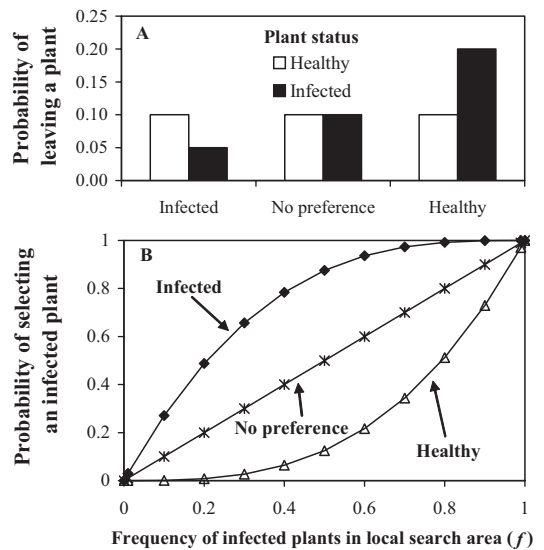


Fig. 1. (A) With feeding preference for infected plants, the probability that an insect left an infected plant was decreased by two-fold. With feeding preference for healthy plants, the probability that an insect left an infected plant was increased by two-fold. The probability that an insect left a healthy plant remained constant. (B) With orientation preference, insects were more likely to select infected or healthy plants. This was accomplished by setting the probability that an infected or healthy plant was selected to a value that was greater or less than the frequency of infected plants in the local search area (f). Probabilities were calculated using equations 1 and 2.

plant depended on their preference for that plant type. Thus, feeding preference for infected plants was simulated by decreasing the probability that an insect left an infected plant by two-fold (Fig. 1A). Similarly, feeding preference for healthy plants was simulated by increasing the probability that an insect left an infected plant by two-fold (Fig. 1A). The probability that an insect left a healthy plant remained constant.

Orientation Preference. With orientation preference, an insect was more likely to select and move onto an infected or healthy plant, depending on its preference. Orientation preference for infected plants was simulated by setting the probability that an infected plant was selected to a value that was greater than the frequency of infected plants in the local search area (Fig. 1B). With orientation preference for infected plants, the probability that an infected plant was selected was

$$1 - (1 - f)^{p_i} \quad [1]$$

where f was the proportion of infected plants in the local search area, and p_i represents the degree of preference for infected plants. For simulations presented here, p_i was assigned a value of 3.

Orientation preference for healthy plants was simulated by setting the probability that an infected plant was selected to a value that was less than the frequency of infected plants in the local search area (Fig. 1B). Thus, with orientation preference for healthy plants, the probability that an infected plant was selected was

$$f^{p_h} \quad [2]$$

where f was the proportion of infected plants in the local search area and p_h represents the degree of preference for healthy plants. For simulations presented here, p_h was set to 3.

Acquisition and Inoculation. If an inoculative insect landed on a healthy plant, it had a fixed probability of transmitting the pathogen to the plant for each time step it remained on that plant (default value = 0.50). Likewise, if a pathogen-free insect landed on an infected plant, it had a fixed probability that it would acquire the pathogen for each time step that it remained on that plant (default value = 0.50). If a plant was inoculated, it took a specified number of times steps for symptoms to develop (referred to as the "latent period"; default value = 1 time step). Insects showed preference or aversion to symptomatic infected plants, but not to asymptomatic infected plants. Insects could acquire the pathogen only from symptomatic plants. Insects were able to transmit the pathogen immediately after acquisition and the pathogen persisted for a specified number of time steps in the insect (referred to as "persistence"; default value = indefinitely). For simplicity, infected plants were assumed to be unable to recover from the pathogen and were not removed.

Simulations. Simulations were run as a 3 by 3 factorial, pairing each level of feeding preference (i.e., preference for healthy, no preference, or preference for infected) with each level of orientation preference

(i.e., preference for healthy, no preference, or preference for infected). First simulations were run with default parameter values (Table 1) to describe the basic effects of each combination of feeding preference and orientation preference. Then sensitivity analyses were used to determine the conditions under which the effects described by initial simulations produced qualitatively different results. This was accomplished by systematically varying each parameter to a value greater than or less than the default value while holding all other parameters at their default value (Table 1). In total, 117 unique parameter combinations were investigated.

Results

Simulations with Default Parameters. Without feeding or orientation preference, the relative rate of pathogen spread was dependent on the percentage of infected plants (Fig. 2E). Initially, the spread of the pathogen was slow because few insects were inoculative and few plants were infected (Fig. 3E). The rate of pathogen spread reached a maximum when $\approx 25\%$ of plants were infected and remained at that rate until $\approx 75\%$ of plants were infected (Fig. 2E). The rate of pathogen spread decreased when a high proportion of plants were infected because inoculative insects mainly moved between plants that were already infected (Fig. 2E).

Feeding preference did not alter the qualitative relationship of the percentage of plants infected with the rate of pathogen spread, but it did alter the overall rate of pathogen spread (Fig. 2B, E, and H). Feeding preference for healthy plants increased rates of pathogen spread compared with simulations with no preference because insects spent less time on infected plants (compare Fig. 2B–E). Feeding preference for infected plants decreased rates of pathogen spread compared with simulations with no preference because insects spent longer periods on infected plants (compare Fig. 2H to E). Consequently, the pathogen spread faster with feeding preference for healthy plants than with feeding preference for infected plants (Fig. 3B and H). The rate effects described for feeding preference were observed regardless of which type of orientation preference it was paired with (Figs. 2 and 3).

With orientation preference, the type of plant preferred (i.e., healthy versus infected) altered the qualitative relationship of the percentage of plants infected with the rate of pathogen spread (Fig. 2). Specifically, orientation preference for healthy plants led to the highest rates of pathogen spread when most plants were infected (Fig. 2D), whereas orientation preference for infected plants led to the highest rates of pathogen spread when most plants were not infected (Fig. 2F). With orientation preference for healthy plants, pathogen spread was initially slow (Figs. 2D and 3D) because most insects were not inoculative and avoided the few infected plants in the field. Once a sufficient number of insects had acquired the pathogen, it spread through the field

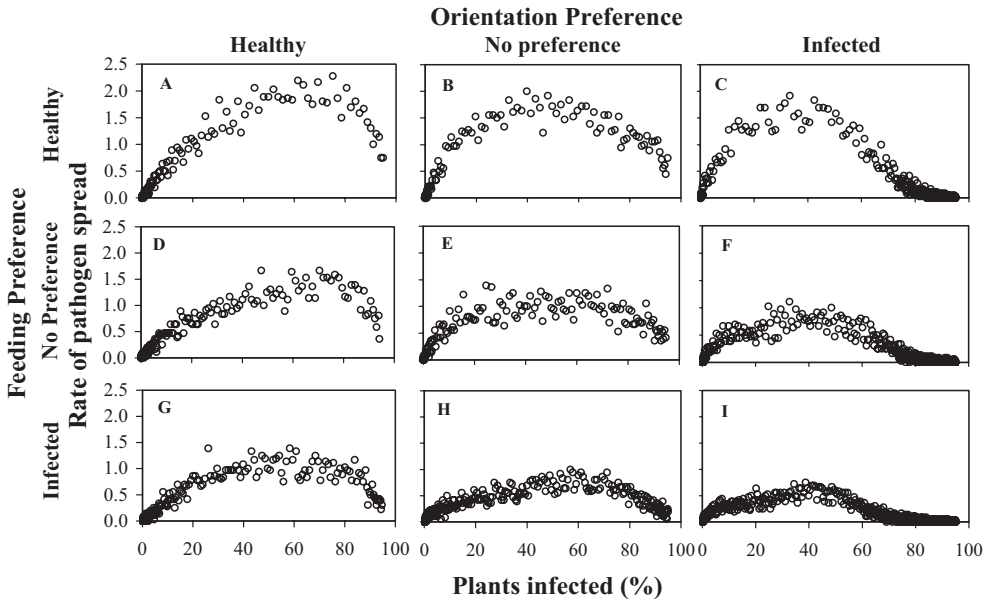


Fig. 2. Relationship of the percentage of plants infected with the rate of pathogen spread for all combinations of feeding preference and orientation preference. The rate of pathogen spread was calculated as the change in the percentage of infected plants per time step. All parameters were set to their default values.

quickly as inoculative insects preferentially moved to healthy plants (Figs. 2D and 3D). Accordingly, rates of pathogen spread were fastest when >50% of plants were infected (Figs. 2D and 3D). In contrast, with orientation preference for infected plants, pathogen spread was initially fast (Fig. 3F), but then slowed once most plants were infected (Figs. 2F and 3F). The pathogen spread quickly at first because

insects acquired the pathogen at a high rate because they were attracted to the few infected plants in the field. However, once most plants were infected, the pathogen spread slowly as insects predominately moved between infected plants. Accordingly, rates of pathogen spread were fastest when <50% of plants were infected (Fig. 2F). The qualitative effects of orientation preference were observed re-

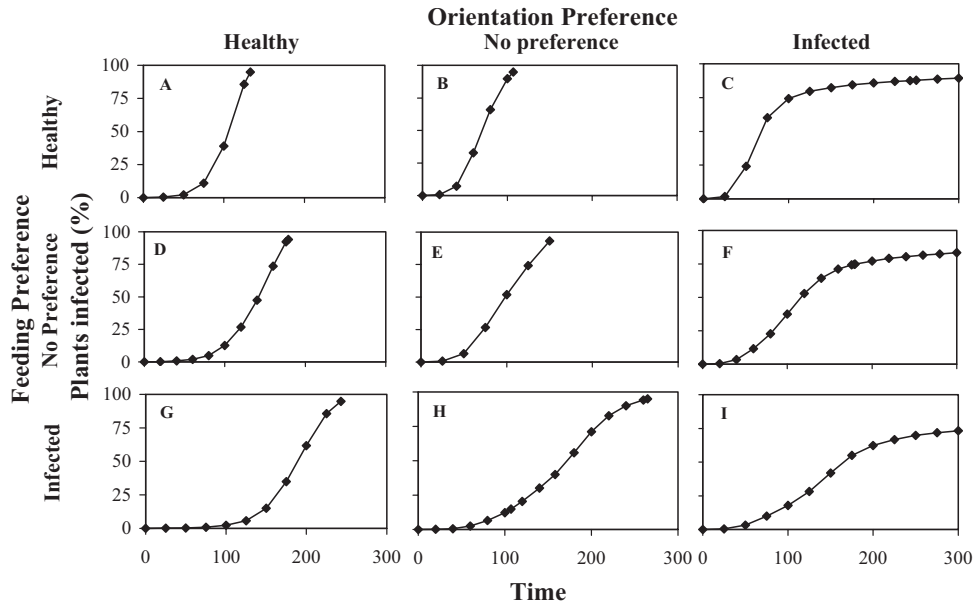


Fig. 3. Percentage of infected plants over time for all combinations of feeding preference and orientation preference. Simulations were run until 95% of plants were infected, however only 300 time steps are shown here. All parameters were set to their default values.

ardless of which type of feeding preference it was paired with (Figs. 2 and 3).

Sensitivity Analysis. Increasing or decreasing the initial percentage of inoculative insects, inoculation rate, acquisition rate, movement rate, or density of insects per plant produced results that were qualitatively similar to those with default parameters (Fig. 2). Lengthening the latent period (i.e., the time between inoculation and onset of symptoms) and shortening persistence (i.e., the length of time an insect remains inoculative) produced qualitatively different relationships between the percentage of plants infected and the rate of pathogen spread than was observed with default parameters for some combinations of feeding preference and orientation preference.

Lengthening the latent period produced qualitatively different results compared with simulations with default parameters, but only with orientation preference for infected plants. In this case, the default assumption of a short latent period (one time step) resulted in decreased rates of pathogen spread when a high proportion of plants were infected (Fig. 4A). Extending the latent period to 60 time steps removed this effect (Fig. 4A). With orientation preference for infected plants and a short latent period, insects predominantly moved between infected plants once most plants were infected, slowing pathogen spread. Lengthening the latent period to 60 time steps removed this effect because the pathogen spread to all plants before most infected plants moved from the asymptomatic to the symptomatic category. Consequently, this effect was dependent on the time required for the pathogen to spread to all plants and the length of the latent period. For example, with low insect density (0.1 per plant) pathogen spread is slow. With slow pathogen spread, there is sufficient time for most infected plants to move from the asymptomatic to the symptomatic category before most plants are infected, even with a long latent period. Thus, with low insect density (0.1 per plant) and a long latent period (60 time steps), the relationship of the percentage of plants infected and the rate of pathogen spread was similar to that observed with default parameters (compare Fig. 2F to Fig. 4B, 0.1 per plant). In contrast, pathogen spread is fast with high insect density (10 per plant). Thus, with high insect density and a long latent period, the pathogen spreads to all plants before asymptotically infected plants move into the symptomatic category, eliminating the aforementioned effect (Fig. 4B, 10 per plant).

Shortening persistence (the length of time an insect remains inoculative) produced qualitatively different results compared with simulations with default parameters, but only with orientation preference for healthy plants. With orientation preference for healthy plants and short persistence (two time steps), epidemics never initiated. This occurred because any insect which initially carried the pathogen was no longer inoculative after two time steps and pathogen-free insects did not acquire the pathogen because they

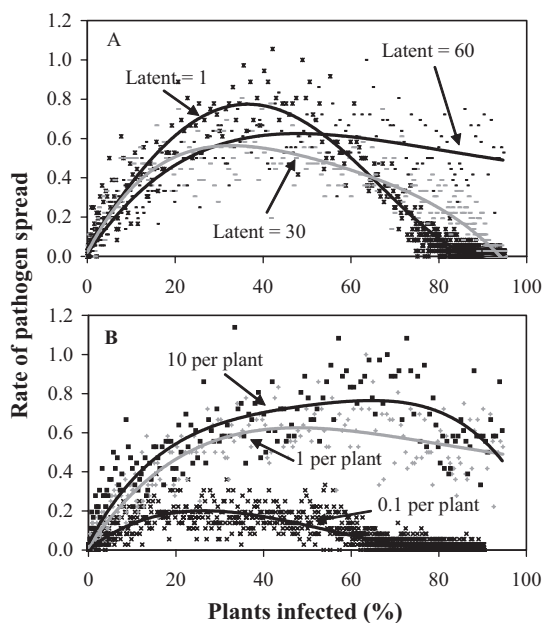


Fig. 4. Effects of orientation preference for infected plants on pathogen spread. (A) Relationship of the percentage of plants infected with the rate of pathogen spread with orientation preference for infected plants and variable latent period. All other parameters were set to their default value. (B) Relationship of the percentage of plants infected with the rate of pathogen spread with orientation preference for infected plants, a long latent period (60 time steps), and variable insect density. All other parameters were set to their default value. Fourth order polynomials were fit to illustrate trends. The x-axis measures the percentage of plants infected and includes asymptomatic and symptomatic plants. The rate of pathogen spread was calculated as the change in the percentage of infected plants per time step.

avoided the few plants that became infected at the start of the simulation.

As stated above, the magnitude of insect density or insect movement did not alter the effects of preference on the qualitative relationship of the percentage of plants infected with the rate of pathogen spread. However, increasing insect density or insect movement greatly accelerated pathogen spread and reduced the importance of including preference in the model. For example, with low (0.10 per plant) and high (10 per plant) insect density, similar relationships of the percentage of plants infected with the rate of pathogen spread were observed for each type of feeding preference (Fig. 5A and B). However, with low insect density, the type of plant preferred had a large effect on the number of time steps required to reach 95% of plants infected, whereas with high insect density the type of plant preferred had little effect (compare Fig. 5C to D). Thus, the magnitude of insect density or insect movement is likely to have greater effects on pathogen spread than insect preference for healthy or infected plants.

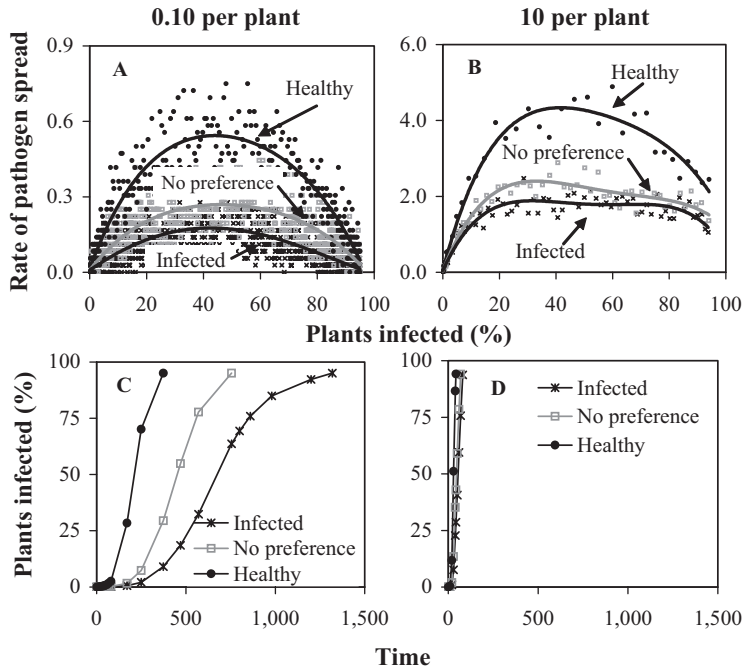


Fig. 5. Effects of feeding preference on the relationship of the percentage of plants infected with the rate of pathogen spread with low (A) and high (B) insect density. Fourth order polynomials were fit to illustrate trends. Effects of feeding preference on the absolute time required for the pathogen to spread through the field with low (C) and high (D) insect density. All other parameters were set to their default value.

Discussion

Feeding preference and orientation preference affected pathogen spread differently (Figs. 2 and 3). Feeding preference tended to increase or decrease the overall rate of pathogen spread, but it did not alter the qualitative relationship of the percentage of plants infected with the rate of pathogen spread. In contrast, orientation preference had little effect on the overall rate of pathogen spread, but it altered the qualitative relationship of the percentage of plants infected with the rate of pathogen spread. Long latent periods altered the effect of orientation preference for infected plants (Fig. 4A), but not the effect of orientation preference for healthy plants. These results illustrate the importance of elucidating the mechanisms responsible for vector preference and indicate that the time period over which insects respond differentially to healthy and infected plants can have important effects. Finally, the results also indicate that the magnitude of insect density or insect movement is likely to have a larger effect on the time required for a pathogen to spread through a field than insect preference (Fig. 5C and D).

The model used here and the model used by McElhany et al. (1995) were simple and their limiting assumptions should be highlighted. Insect population dynamics and recurrent emigration into the field were excluded from the models for simplification. Doing so provides greater focus on assumptions about insect response to healthy and infected plants. However, as

the models lack biological realism they are not suitable for predicting the progress of real epidemics. Nonetheless, the format used by both models provides a valuable means for gaining insight into the effects of insect preference on pathogen spread.

With regard to feeding preference, response to healthy plants was assumed to be fixed and movement from infected plants was increased or decreased to simulate feeding preference for healthy or infected plants, respectively (Fig. 1A). This assumption was chosen because a priori insects are expected to respond consistently to healthy plants and in empirical tests movement of insects from infected plants is expected to be measured relative to that of healthy plants. It is possible, however, for simulations to be completed with the alternative assumption of fixed movement from infected plants and increased or decreased movement from healthy plants. Simulations of feeding preference under this alternative assumption produced no clear differences between simulations without preference and simulations with feeding preference for infected or healthy plants.

Several studies indicate that vectors may use visual and olfactory orientation cues to discriminate between healthy and infected plants. As stated previously, preference for infected plants is often hypothesized to be due to the yellowing of leaves caused by infection (Ajayi and Dewar 1983, Eckel and Lampert 1996, Fereres et al. 1999, Marucci et al. 2005). This hypothesis is supported by studies demonstrating

greater landing rates of alighting aphids on infected plants compared with healthy plants in some systems (Ajayi and Dewar 1983, Eckel and Lampert 1996), although this is not always the case (Ferreles et al. 1999). The use of short-range olfactory cues also has been shown to be important in the discrimination process in some systems (Eigenbrode et al. 2002, Jiménez-Martínez et al. 2004, Srinivasan et al. 2006). The use of long-range olfactory cues to differentiate between healthy and infected hosts seems to be undocumented for insect vectors of plant pathogens. This may be due to the focus of many studies on aphid species, which are typically weak flyers and unlikely to follow odor plumes to a source. However, the use of long-range olfactory cues has been demonstrated for insect vectors of animal pathogens. Lacroix et al. (2005) demonstrated that *Anopheles gambiae* Giles s.s. showed greater attraction to humans infected with *Plasmodium falciparum* in the transmissible stage relative to healthy humans and humans infected with the asexual stage of the pathogen.

In some systems, gustatory cues may be required for insects to discriminate between healthy and infected plants, providing the opportunity for acquisition and transmission of the pathogen during the discrimination phase. Evidence for such effects appears to be mostly inferential. For example, Macias and Mink (1969) found no difference in the choice of apterous *Myzus persicae* (Sulzer) for sugar beet (*Beta vulgaris* L.) infected with one of two yellows viruses (beet western yellows virus and sugarbeet yellows virus) versus healthy sugar beet when insect settling on whole plants was compared. However, preference for infected plants was found in tests using excised leaves held in proximity. Macias and Mink (1969) argued that apterous *M. persicae* were able to sample multiple leaf types in the excised leaf experiment, but not in the whole plant experiment. Thus, they suggested that feeding was required to distinguish between healthy and infected plants. In another study, Blua and Perring (1992) compared emigration rates of alate *Aphis gossypii* Glover placed on zucchini infected with zucchini mosaic virus and healthy zucchini (*Cucurbita* spp.). They found that emigration rates of *A. gossypii* placed directly onto plants was greater when insects were placed on plants infected for 4 wk than when *A. gossypii* were placed on healthy plants or asymptomatic plants infected for 2 wk. Using an electronic feeding monitor, Blua and Perring (1992) found that feeding behavior of *A. gossypii* differed on healthy and infected hosts. Thus, they inferred that emigration occurred after host evaluation by the insect.

The structure of the model presented here was based on the spatially explicit model of McElhany et al. (1995). Preference in the model of McElhany et al. (1995) was analogous to our simulations with both types of preference working in conjunction (Fig. 2A and I). Specifically, they assumed that insects were more likely to move off of infected or healthy plants depending on their preference, similar to how feeding

preference was modeled here. After leaving a plant, the insect began a random walk, evaluating each plant it encountered and was more likely to come to rest on the type of plant it preferred. Acquisition and transmission of the pathogen was assumed to occur only after the insect had finished the random walk. Thus, this phase of the movement process was similar to how orientation preference was modeled here. The results shown here indicate that the qualitative effects of orientation preference on pathogen spread are observed regardless of the type of feeding preference it was paired with (Fig. 2). Thus, the results of McElhany et al. (1995) are qualitatively similar to the effects of orientation preference seen here.

In another simulation model, Real et al. (1992) modeled the spread of anther smut fungus, *Ustilago violacea*, by bumblebees. In this model, bumblebees preferred healthy flowers over infected flowers and could discriminate between healthy and infected flowers before visiting them. Similar to simulations with orientation preference for healthy plants (Fig. 2D), Real et al. (1992) found that pathogen spread was slower with preference for healthy flowers compared with no preference, but only when <10% of flowers were infected. Using a different approach, Kingsolver (1987) examined the effects of mosquito preference for hosts with malaria with a set of compartmentalized differential equations and found that preference for infected hosts increased the range of parameter space over which the pathogen could persist.

Simulations with feeding preference and orientation preference affected pathogen spread differently (Fig. 2). This occurred because there are two key differences between feeding and orientation preference. First, the use of visual or olfactory orientation cues precludes the possibility of acquisition and transmission of the pathogen during discrimination between healthy and infected plants, whereas the use of gustatory feeding cues does not. Second, feeding preference results in increased or decreased movement between plants, whereas orientation preference does not. Consequently, a thorough understanding of the mechanisms responsible for preference is required to make inferences about the effects of preference on pathogen spread.

Acknowledgments

I thank Kendra Baumgartner, Steve Castle, Edwin Civerolo, Aaron Gassmann, Fred Gould, Russell Groves, Hannah Nadel, Brendon Reardon, and Drake Stenger for comments on an earlier draft of this manuscript.

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Received 14 September 2007; accepted 15 September 2007.